Is over-imitation a uniquely human phenomenon? Insights from human children as compared to bonobos

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Abstract

Imitation is a key mechanism of human culture and underlies many of the intricacies of human social life, including rituals and social norms. Compared to other animals, humans appear to be special in their readiness to copy novel actions as well as those that are visibly causally-irrelevant. This study directly compared the imitative behavior of human children to that of bonobos, our understudied great ape relatives. During an action-copying task involving visibly causally-irrelevant actions, only 3-5 year old children (N = 77) readily copied whereas no bonobo from a large sample did (N = 46). These results highlight the distinctive nature of the human cultural capacity and contribute important insights into the development and evolution of human cultural behaviors.

Debate over the uniqueness of human culture and the role that imitation plays in its evolutionary and ontogenetic development has become the focus of increasing research attention (Caldwell & Millen, 2009; Meltzoff & Prinz, 2002; Tennie, Call, & Tomasello, 2009; Tomasello, 1999; Whiten, 2016). In particular, comparative research has attempted to identify what makes human culture special as compared to that of other great apes, and to identify similarities and differences in the underlying social learning mechanisms (Tomasello, 1996; Tomasello, Savage-Rumbaugh, & Kruger, 1993; Vale et al., 2016; Whiten, 2013; 2016). Imitation, which in this paper we define as the faithful copying of others' body movements, has elicited particular attention as it has been proposed to form a

core component of human culture, enabling the acquisition of causally opaque material culture and action-based cultures (e.g. gestures and dance) as well as contributing to their accumulation over time (Acerbi & Tennie, 2016; Dean et al., 2012; Gergely & Csibra, 2006; Tennie et al., 2009, but see Caldwell & Millen, 2009; Caldwell, Schillinger, Evans, & Hopper, 2012; Morin, 2015). Imitation is also involved in many of the complexities of human social life, including for norms, rituals and conventions (Legare & Nielsen, 2015; Legare & Watson-Jones, 2015; Meltzoff & Prinz, 2002; Rakoczy, Warneken, & Tomasello, 2008).

A striking feature of human imitation is the extent to which humans are prepared to imitate actions that appear causally-irrelevant (Horner & Whiten, 2005; Lyons, Young, & Keil, 2007; McGuigan, Whiten, Flynn, & Horner, 2007). This phenomenon, termed 'over-imitation', emerges early during childhood (Lyons, Young & Keil, 2007; Over & Carpenter, 2012). It occurs in both Western and non-Western cultures (Berl & Hewlett, 2015; Nielsen & Tomaselli, 2010) and gradually increases with age, starting from around three years old (McGuigan, Gladstone & Cook, 2012; McGuigan, Makinson & Whiten, 2011; McGuigan, Whiten, Flynn, & Horner, 2007). Over-imitation is thought to underlie many human socio-cultural behaviors including ritual and other forms of normative behavior (Legare & Nielsen, 2015; Legare & Watson-Jones, 2015; Nielsen, Kapitány, & Elkins, 2015). It is also involved in cumulative technological culture, thus, it was suggested that children's over-imitation is driven by their need to learn about causally-opaque cultural artefacts (Lyons et al., 2007). This may be especially important in cases where cultural accumulation has led to artefacts whose causal properties have become complex and opaque, i.e. copying is required to produce or use them (Gergely & Csibra, 2006; Lyons et al., 2007; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Nevertheless, recent research has shown that over-imitation is strongly motivated by social factors, such as to affiliate with or 'be like the other'

(Keupp, Behne, & Rakoczy, 2013; Nielsen, 2006; Nielsen & Blank, 2011) and to conform to perceived conventions and norms (Herrmann, Legare, Harris & Whitehouse, 2013; Keupp et al., 2013; Legare & Nielsen 2015). For instance, children are more likely to copy when the task is framed as being normative (Keupp et al. 2013; Legare & Nielsen, 2015; Moraru, Gomez & McGuigan, 2016), and after being primed with third-party ostracism (Over & Carpenter, 2009a, 2009b). They can infer friendship and social status from watching others imitate (Over & Carpenter, 2015) and trust individuals more that have imitated them (Over, Carpenter, Spears, & Gattis, 2013).

The study that originally reported over-imitation (Horner & Whiten, 2005) contrasted children's copying with an apparent absence of this behavior in captive chimpanzees, a finding which has since been replicated for orangutans (Nielsen & Susianto, 2010). Children were willing to insert a stick into both an opaque and a clear box in order to retrieve a reward, even though the insertion in the latter was visibly causally-irrelevant. Although this influential study has stimulated a plethora of studies, it is limited in its ability to detect over-imitation in the sense in which we define it here (i.e. with a focus on action copying). This is because pure action-copying could not be distinguished from other forms of social learning due to the fact that the captive chimpanzees were already competent stick-users. In other words, this stick-based task could detect copying of the location of the stick insertion, rather than copying the action itself. Thus, for both the apes and the children, this task more accurately tested "local over-enhancement" and/or over-emulation learning (see Tennie, Call, & Tomasello, 2006 for discussion). Note this experiment also involved a "two-target task", where objects could be moved to one of two sides. Copying here was likewise likened with imitation; however, while this task controlled for local enhancement, it could not fully pinpoint action-based imitation as it could not exclude the so-called 'object-movement

reenactment' (Custance, Whiten, & Fredman, 1999; Heyes & Ray, 2000). Later studies, which added actions that neither changed nor moved objects, were generally unable to find action-copying in chimpanzees (Tennie, Call & Tomasello, 2012), but found it in children (Legare, Wen, Herrmann & Whitehouse, 2015).

Given these constraints and the fact that no equivalent data is yet available for the capacities of our other closest living relative, the bonobo (*Pan paniscus*), the question of whether over-imitation is uniquely human among the great apes remains unresolved. Nevertheless, it is acknowledged that some animals will copy some actions under certain conditions (Huber et al., 2009). This includes, for example, the so-called 'Do as I do' studies which involve heavily-trained animals (Call, 2001; Custance, Whiten, & Bard, 1995; Miles, Mitchell, & Harper, 1996). There is also evidence from 'enculturated' great apes that have received extensive experience in human-centered environments (Bjorklund, Bering, & Ragan, 2000; Buttelmann, Carpenter, Call & Tomasello, 2007; Byrne & Tanner, 2006; Call, 2001; Carrasco, Posada, & Colell, 2009; Hayes & Hayes, 1952; Miles et al., 1996). Importantly however, the extent to which ecologically-relevant animals – i.e. those that are untrained and un-enculturated– spontaneously copy actions remains hotly debated (Whiten, 2016; Whiten, Custance, Gomez, Teixidor, & Bard, 1996; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Zentall, 1996, 2006). The lack of resolution is partly due to methodological constraints in distinguishing imitation from other social learning processes (Heyes & Ray, 2000; Tennie et al., 2006).

To date, most research on great ape social learning has focused on 'two-target' tasks involving experimental puzzle boxes that can be opened in more than one way in order to retrieve a reward (Horner & Whiten, 2005; Horner, Whiten, Flynn, & de Waal, 2006;

Whiten, Horner, & de Waal, 2005; Whiten et al., 1996; Whiten, McGuigan, Marshall-Pescini & Hopper, 2009). While two-target tasks provide many key insights into the factors shaping animal cultural transmission (Galef, 2015; Whiten, 2016), they cannot clearly distinguish imitation from other learning mechanism due to the fact that the demonstrator movements are confounded with the object movements (Custance, Whiten, & Fredman, 1999; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Whiten et al., 2009). Thus, animals can plausibly solve the tasks via emulation, which is the copying of results of actions on the environment (Heyes & Ray, 2000; Tennie et al., 2006). Moreover, given that chimpanzees are able to copy the movements of the apparatus in two-target tasks without seeing actions leading to these results (Hopper, Lambeth, Schapiro & Whiten, 2008), emulation cannot be ruled out. Successful performance on two-target tasks (Custance et al., 1999) is also widespread in the animal kingdom (Galef, 2015; even in reptiles, Kis, Huber & Wilkinson, 2015), thus limiting its usefulness for determining what truly makes human cultural learning special or why wild great apes, especially chimpanzees and orang-utans, are such expert tool users (Meulman & van Schaik, 2013; Sanz, Call & Boesch, 2013; Whiten et al. 1999;).

Although some great apes will spontaneously copy familiar actions, (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014; Tennie et al., 2012) evidence of *novel* action copying – i.e. which is a core component of human culture - has not been convincingly demonstrated using two-target tasks. This is because the target actions generally always fall within the species-typical repertoire, such as pulling or poking (Tennie et al., 2012). Given the importance of copying novel actions in human culture, it is essential to determine whether great apes can copy novel actions. So far, only two studies with captive chimpanzees have addressed this question, accounting for the various methodological confounds (Tennie et al., 2012; Tomasello et al., 1997). Both tested imitation of novel actions where no physical

126 information about the task was available, i.e. removing the possibility of emulation.
127 Although one of the studies found some evidence of familiar action copying in a single
128 chimpanzee subject (Tennie et al., 2012), neither detected novel action copying in any
129 subject.
130
131 Here, we addressed the confounds of previous studies by designing a paradigm which could
132 test for pure over-imitation, while excluding other social learning mechanisms. We did this
133 by using purely manual gestures as the target actions where no physical information was
134 provided about the solution. In order to probe the potential for over-imitation, some of the
135 target actions were visibly causally-irrelevant. We included target actions that were, to our
136 knowledge, novel or at least very unlikely to be part of a species-typical repertoire.
137
138 To promote the possibility of demonstrating imitation by great apes, we focused our attention
139 to bonobos, a species of great ape that is equally as related to humans as chimpanzees, yet
140 comparatively less studied. For a number of reasons, bonobos may represent a more
141 promising candidate species to demonstrate imitation than chimpanzees. This is because
142 bonobos outperform chimpanzees on socio-cognitive tasks (Herrmann, Hare, Call, &
143 Tomasello, 2010), show enhanced social orientation (Kano, Hirata, & Call, 2015; Kret,
144 Jaasma, Bionda, & Wijnen, 2016) and high levels of social tolerance (Hare & Kwetuenda,
145 2010). Given the inherently social nature of imitation, an activity requiring both social
146 attention and social tolerance, the enhanced social orientation of bonobos may enhance their
147 imitative capacity. The current study explored evidence for pure, spontaneous action
148 imitation in a large sample of untrained and non-enculturated sanctuary-living bonobos as
149 compared to three-to-five year old children. This sample is the largest of its kind ever used
150 with a single great ape species for a pure action imitation study. If lower social tolerance and

the methodological constraints emerging from the nature of previous tasks impede the performance of great apes, we should expect bonobos to show evidence of over-imitation. If over-imitation is a human unique behavior, we should not expect bonobos to copy any of the visibly causally-irrelevant actions.

Method

Participants

Seventy-seven typically-developing children, aged three-to-five years, participated in this study (Mean age= 4.4 years; Range = 3.1–5.9 years; N = 43 males). We selected this age range as children of this age are already manually competent, show reliable evidence of imitation behavior (e.g. Horner & Whiten, 2005; Hopper et al., 2008; McGuigan et al. 2007; Whiten et al., 1996) and are comfortable being tested individually, enabling more cross-species comparisons. Children were recruited from ThinkTank Science Museum in Birmingham, West Midlands, UK and randomly assigned to conditions. Child testing took place between April - December 2016. Using parental questionnaires, we determined that all were typically developing, had normal or corrected to normal vision and spoke English as their first language: 69 children were monolingual, while 8 were bi-lingual (English + Urdu/Punjabi/Spanish/Sinhalese/French/Arabic/Polish). The sample comes from an area of high ethnic diversity consisting of approximately 58% Caucasian, 27% Asian/British Asian, 9% Black/African/Caribbean, 6% Mixed children; the participants came from Working-Middle class backgrounds (estimated from census data for each county, Office of National Statistics, 2011). Five children refused to participate in the task and were excluded from analyses. The remaining children were randomly assigned to one of three conditions (N = 27

175 in the ‘Rub & rotate’ condition (uncommon actions); N = 26 in the ‘Cross & trace’ condition
176 (typical actions) and N = 19 in the Control condition).
177
178 Forty-six non-enculturated and untrained bonobos also participated (Mean age = 11.3 years,
179 Range 3–29 years, N = 25 males). Testing took place in June 2015. The bonobos were
180 housed at Lola ya Bonobo Sanctuary, a naturalistic forested sanctuary, in the Mont Ngafula
181 district, Kinshasa, DR Congo, see SI text for more information. The majority of subjects were
182 orphans, having arrived at the sanctuary as victims of the bush-meat and pet trades. Three
183 were born and mother-reared at the Sanctuary. Following several years of rehabilitation
184 within a cohort group, individuals are integrated into large, mixed-age groups. The majority
185 of our subjects (N = 36) were housed in large, outdoor enclosures. We additionally tested 10
186 juveniles housed in a Nursery. Nursery individuals were cared for by human substitute
187 mothers within a naturalistic forested enclosure with age-matched peers. For subjects from
188 the main enclosures, the experiments were conducted in their sleeping dormitories and before
189 their morning feed in order to maximize motivation. Testing rooms ($15m^2$) had a meshed
190 ceiling with wide bars through which the experimenter could hand items to the subject, which
191 they could then manipulate themselves inside their testing room. In the Nursery, the
192 experiments were conducted face to face with the experimenter within their enclosures and
193 sleeping dormitories.
194
195 Materials and Procedure
196 For all participants, the task involved the opening of a small box (10 x 6 x 3 cm, Figure 1),
197 made of two halves of a single piece of wood. A small chamber was carved out in the middle
198 to place the reward, held in place by a peg-and-hole mechanism.
199

For both test conditions, each participant first took part in a demonstration phase followed by a test phase. All participants were tested individually in a quiet testing area. Children's parents waited behind an occluder so were not visible. All participants observed a human demonstrator who, facing the participant, looked at the box and then slowly performed two consecutive actions onto it, before opening it to reveal the reward inside, which was provided to the participant. Due to health and safety reasons, children received stickers, while bonobos received a food reward (apple piece) – as is typical in such cross-species studies (e.g. Hopper et al., 2008; Herrmann & Tomasello, 2015). This procedure was repeated three times. Between demonstrations, the demonstrator refilled the box behind an occluder, preventing the refilling and closing from being seen.

We tested imitation for actions that we considered plausibly typical or uncommon, based upon our direct observations of actions performed by bonobos and children and our knowledge of their typical manual behaviors. In the 'uncommon' action condition ('Rub-Rotate'), the demonstrator placed the back of the right hand on the top of the box and slowly rubbed it in a clockwise circular motion four times. Next, the demonstrator raised the right hand into the air next to the box and slowly rotated the wrist four times. Given the difficulty in ascertaining whether a demonstrated behavior is truly novel for a long-lived species (Zentall, 2001), we considered these two actions to be 'uncommon' on the basis that, to our knowledge, they had not been previously observed in the study population or any other observed by the authors, and were also unlikely to occur within the species-typical repertoire. We also included a 'typical' action condition ('Cross-Trace'), which included actions that were rare but nevertheless fell within the ape species-typical repertoire, and have also been observed in this bonobo population (Z. Clay, personal observations). Here, the demonstrator held the box (left hand) and with the index finger, slowly traced a diagonal cross across the

top of the box. Next, the demonstrator used this finger to trace around the groove of the box, around its full diameter. There was also a Control Condition (children only), in which everything remained the same except that no target actions were demonstrated.

Following each demonstration, the demonstrator pretended to re-fill the box behind the occluder, but swapped it with a replica box, which was identical in dimensions and external appearance except that it did not actually open (the groove resembled that of the other box, but in reality was not deep enough to open). The use of a replica maximised the chances of observing imitation once species-typical solutions were discovered to be ineffective.

During the test phase, each participant was provided with a replica box, without verbal instruction. Participants were given up to two minutes to interact with the box. Regardless of performance, all participants were rewarded at the end of the trial. Trials were videotaped using a digital Sony Handy-camcorder mounted on a tripod.

Coding

The occurrence of accurate matches of any of the four demonstrated actions was coded from video (yes or no). A second coder, blind to the hypotheses and conditions re-coded 25% of the videos. Inter-observer reliability across all conditions was excellent (Cohen's Kappa = 0.94, SE = 0.05). Full details of coding protocol are provided in the SI Text.

Ethical statement

We received ethical clearance from the University of Birmingham Ethical Review Committee (ERN_13-1412) and the Marie Curie European Commission Ethical Screening Program (n° 628763). This study conformed to University of Birmingham's Code of Practice for

Research. For children, we received full approval and ethical clearance from ThinkTank Museum and full informed consent from parents. For the bonobos, we received full ethical approval to conduct this study from 'Les Amis des Bonobos du Congo' (ABC, Lola ya Bonobo Sanctuary). This study complied with all legal requirements required for conducting research in DR Congo (Research permit: MIN.RS/SG/180/011/2016).

Results

We observed high levels of spontaneous imitation by children across both uncommon ('Rub –Rotate') and typical ('Cross-Trace') action conditions. The majority of children readily copied at least one the two observed actions in both conditions (Rub-Rotate: 77.8% of children (21/27); Cross & Trace: 81% of children (21/26)). Of these children, approximately one third spontaneously copied both actions demonstrated to them (Rub-Rotate: 39% children (8/27); Cross & Trace: 27% children (7/26)), see Figure 2. For cases where children only copied one of the two actions, in both conditions it was most often the second action which was copied, suggesting a working memory constraint and/or a recency effect (for single action responses, copying of the second demonstrated action occurred in 10/13 cases for Rub-Rotate and 12/15 cases for Cross-Trace). During a Control condition, where everything remained the same except that no demonstration was performed, no child (N = 19) performed any of the target actions. In all cases of copying, the children copied the demonstrated (causally-irrelevant) actions first, before potentially performing any causally-relevant actions to open the box (i.e. prying open the box).

In contrast, no bonobo in our sample copied any of the target actions in either condition. Instead, they attempted to open the box using an array of causally relevant, species-typical

methods, which included pounding, biting, kicking and shaking. As no bonobo demonstrated any of the actions, we did not run a Control condition for the bonobos.

Requests for assistance occurred in both species, but more in children, which is not surprising given their language skills. Fourty-eight percent (14/29) of children made direct verbal requests (e.g. “It’s too hard for me, can you do it?”) and/or gestural requests. Although actively returning things objects in one’s possession is not typically observed in great apes, 21.8% of bonobos (10/46) in our sample actively returned the box to the experimenter after attempting to open it; thus outwardly resembling a request for assistance.

Discussion

Our study identified striking contrasts in young children’s copying behavior as compared to that of bonobos, our closest living relatives. Children readily copied the actions, which were visibly causally-irrelevant, whereas not a single bonobo did. Whether or not the bonobos were unable, unwilling, or both, to copy, the results highlight striking differences in human children’s cultural behaviors as compared to those of great apes. Importantly, our study addressed methodological constraints of previous studies, thus providing a true test for over-imitation which allowed us to compare the performances of both children and great apes. Combining our results with earlier findings for chimpanzees (Tennie et al., 2012; Tomasello et al., 1997), our findings indicate that bodily over-imitation – at least in high frequencies – is a uniquely human capacity, which likely plays a key role in explaining why human culture can accumulate over time.

This study focussed on bonobos, an understudied species of great ape that might be expected

to show higher imitative potential than chimpanzees, given their enhanced social orientation (Kano et al., 2015; Kret et al., 2016) and high social tolerance (Hare & Kwetuenda 2010). The fact that the bonobos failed to over-imitate demonstrates that even enhanced social orientation may not be enough to trigger human-like cultural learning behaviors. These results thus demonstrate an important qualitative difference between humans and great apes in regards to the capacity or motivation to copy visibly causally-irrelevant actions. Differences in the capacity for action-copying may relate to cognitive constraints in great apes' abilities to understand goals and intentions as humans do (Call & Tomasello, 2008). Differences in motivation are likely to relate to the strong affiliative and normative drivers of imitation in humans but not in great apes (Over & Carpenter, 2012; Legare & Nielsen, 2015).

An alternative explanation to the lack of copying by the apes is that it was due to methodological constraints. However, although small sample size is frequently a critique of great ape studies, this was not the case for our study. The combined results from the two related studies also make this explanation unlikely for chimpanzees (Tennie et al., 2012; Tomasello et al., 1997). Age is also unlikely to be an explanatory factor, given that a full age range was tested, and no subject showed evidence of copying. Another possibility is that using a human demonstrator inhibited the bonobos' motivation to imitate. However, a conspecific demonstrator was used in both chimpanzee studies (Tennie et al., 2012; Tomasello et al., 1997), yet no novel action copying occurred. Moreover, in a review of 23 studies directly comparing chimpanzee and human performance in experimental settings, Boesch (Boesch, 2007) concluded that the use of human demonstrators did not seem to influence observed species differences. Lack of motivation also does not appear to be a problem: the majority of apes persisted in this task and employed many alternative techniques while trying to open the box.

Although previous studies have shown that great apes will sometimes copy in certain circumstances, it appears to primarily occur after receiving extensive training and/or enculturation (Bjorklund et al., 2000; Byrne & Tanner, 2006; Call, 2001; Carrasco et al., 2009; Custance, Whiten, & Bard, 1995; Hayes & Hayes, 1952; Miles, Mitchell, & Harper, 1996). Given that these factors are absent in wild apes, ecologically relevant findings must therefore come from untrained and un-enculturated apes. In our study, not a single untrained and non-enculturated bonobo copied any of the demonstrated actions, thus providing qualitative and ecologically-valid evidence of the distinctive nature of the human cultural capacity as compared to that great apes: the copying of visibly causally-irrelevant actions (especially novel actions) appears to be uniquely human.

One relevant question is why children were so willing to copy these superfluous actions? It has been suggested that children copy in a blanket fashion due to the causal-opaqueness of a task (Horner & Whiten, 2005; Lyons et al., 2007). However, children's over-imitation is also influenced by social motivations, such as to socially bond (Over & Carpenter, 2012) or conform to perceived rituals or norms, which are themselves initially opaque (Kenward, 2012; Kenward, Karlsson, & Persson, 2011; Hermann et al., 2013; Keupp et al., 2013; Legare & Nielsen 2015). The main answer therefore is likely to be the hyper-social nature of humans as compared to other animals (Claidiere, Bowler & Whiten, 2011; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012; Tomasello, 2014). The fact that the adult demonstrator remained present during the test phase in our study is likely to have enhanced the children's motivation to copy (Harris, 2012; Nielsen & Blank, 2011; Tomasello, 2014). It is well known that children are more likely to copy causally-irrelevant actions performed by adults as compared to by peers (Flynn, 2008; Horner & Whiten, 2005; McGuigan et al., 2011; Wood,

Kendal & Flynn, 2012). Children are also more likely to copy in the physical presence of adult observers as compared to if they leave the room (Nielsen & Blank, 2011). In this regard, young children in this study may have perceived the presence of an adult observer during the imitation phase as an implicit cue to over-imitate. While this may be the case, it could be likewise expected that over-imitation in great apes would be also be more likely to occur within an observer's presence. The striking absence of over-imitation for the bonobos even in such a context thus further highlights the apparently stark species differences that exist in this cultural capacity.

In sum, our results highlight profound differences in the cultural behaviors of human children as compared to great apes. The copying of causally-irrelevant actions represents a core component for both material and social cultures in human, and thus the striking difference between children and great apes in this regard provides critical insights into why both the diversity and frequency of human cultural behaviors differ so vastly differ compared to that of other great apes (Acerbi & Tennie, 2016).

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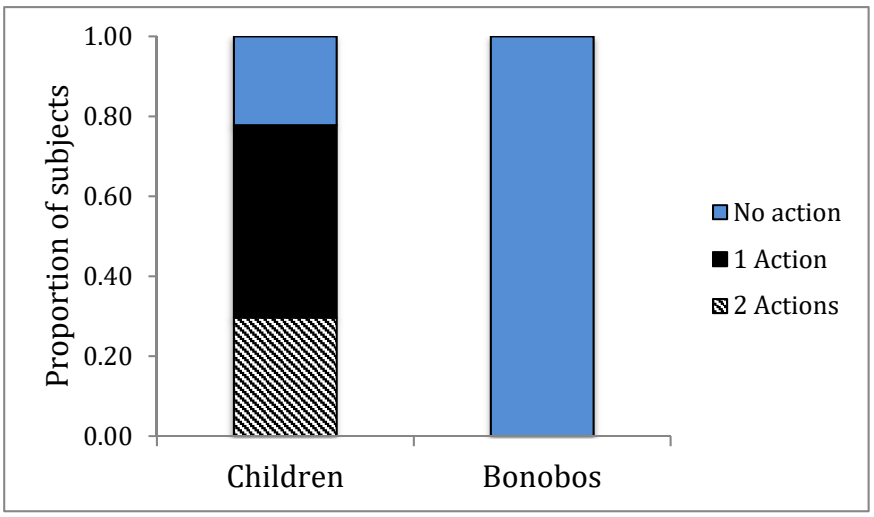
Figure Captions

Figure 1. Image of the wooden box stimuli used in the imitation experiment (also showing a reward sticker provided to child participants)

Figure 2. Results showing proportion of child (N = 52) and bonobo (N = 46) participants that spontaneously imitated the observed actions in the (A) Uncommon ("Rub-rotate") condition and the (B) Typical ("Cross-trace") condition.

Figures

Figure 1.


1.00
0.80
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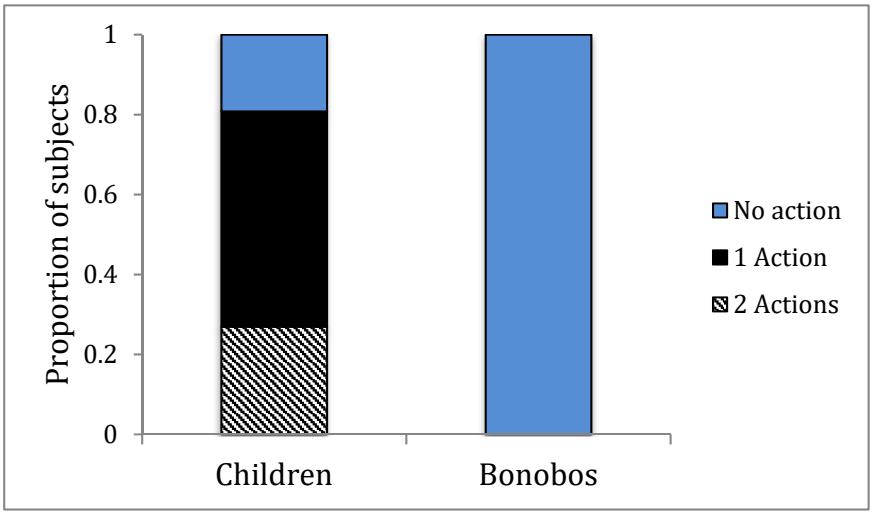
Proportion of subjects
Children
Bonobos
No action
1 Action
2 Actions

A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0.8
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0.4
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Proportion of subjects
Children
Bonobos
No action
1 Action
2 Actions

B

Figure 2.